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An investigation of ecological correlates with hand and foot morphology in callitrichid primates.

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ABSTRACT

Studies of primate taxomony and phylogeny often depend on comparisons of limb dimensions, yet there is little information on how morphology correlates and contributes to foraging strategies and ecology. Callitrichid primates are ideal for comparative studies as they exhibit a range of body size, limb proportions and diet. Many callitrichid species exhibit a high degree of exudativory and to efficiently exploit these resources they are assumed to have evolved morphologies that reflect a level of dependence on these resources. We tested assumptions by considering measurements of limb proportion and frictional features of the volar surfaces in preserved specimens of 25 species with relation to published life history and ecological data. The degree of exudativory and utilization of vertical substrates during foraging were found to correlate both with size and with size-corrected foot and hand dimensions. Smaller species, which engage in greater degrees of exudativory, had proportionally longer hands and feet and more curved claw-like tegulae (nails) on their digits to facilitate climbing on vertical substrates. The density of patterned ridges (dermatoglyphs) on the volar surfaces of the hands and feet is higher in more exudativorous genera, suggesting a role in climbing on vertical tree trunks during foraging. Dermatoglyph comparisons suggest that ridges on the soles and palms may facilitate food procurement by enhancing frictional grip during exudate feeding. Volar pad features corroborate taxonomic relationships described from dental morphology.

Callitrichidae (Mammalia: Primates) includes over forty diverse species of New World Monkey. These may be grouped into 'marmosets' (*Callibella, Callimico, Callithrix, Cebuella,* and *Mico*) or tamarins (*Leontopithecus* and *Saguinus*) (Rylands et al., 2012). Prior to the reassessment of taxonomic relationships by Rylands et al., (2000) and the subsequent recognition of *Callibella* as a separate species (Van Roosmalen and Van Roosmalen, 2003), *Callithrix* was the most diverse genus, with over twenty species. Since 2003 *Callibella, Callimico* and *Cebuella* have been considered monotypic and fourteen species have been removed from *Callithrix* to a new genus *Mico,* thereby making *Saguinus* the most diverse callitrichid genus (Rylands et al., 2012). Recent analysis of phylogenetic relationships in all primates (Perelman et al. 2011) further confirms the taxonomy described in Cortés-Ortiz (2009): (*Saguinus* (*Leontopithecus* (*Callimico* (*Callithrix* (*Callibella* (*Cebuella*/*Mico*)))))). Although their taxonomy is under seemingly constant review, callitrichids are ideal subjects to investigate morphology and allometry trends in relation to ecology because they represent a wide range of body sizes and exhibit variability in diet and foraging strategies both between and within genera, despite close phylogenetic proximities.

Phylogeny and taxonomy of primates often depend on comparing limb proportions and morphology (i.e. Falsetti et al., 1993; Shoshani et al., 1996; Anderson et al., 2000; Schmidt, 2005, 2008). The relationships between primate locomotor modes (i.e. vertical clinging and leaping, quadrupedalism and bipedalism) and post-cranial morphology are well-known (e.g. Anenome, 1990; Gebo, 1996; Lemelin and Schmitt, 1998; Garber and Leigh, 2001; Anapol et al., 2005; Schmidt, 2005; Wright, 2007; Schmidt, 2008).

While diverse morphologically and ecologically, most callitrichids have a common trait of consuming plant exudates, principally gums (see Smith, 2010). Consequently, many species

possess unique features that allow them to efficiently utilize this nutrition-poor, difficult to access resource including specialist digestive systems in *Mico* (*Callithrix*) *emiliae* (Ferrari and Martins, 1992), gouging incisors, and other craniofacial characteristics in *Callithrix*, *Cebuella* and *Mico* (Forsythe & Ford, 2011). All callitrichids have elongated, laterally compressed and hooked claw-like nails or 'tegulae' (Garber, 1980, Thorndike, 1968; Soligo and Müller, 1999). Though originally considered a primitive character, it is now assumed that callitrichid tegulae are a derived specialization which facilitate the gum-feeding behavior prevalent in the marmosets and tamarins (Garber and Sussman, 1984; Sussman and Kinzey, 1984; Hamrick, 1998; Soligo and Müller, 1999). Garber et al. (1996) identified two major problems with this inference: firstly, although the presence of 'claws' may be expected to aid vertical clinging, the postural behavior most commonly associated with gum-feeding (Garber, 1992, 1993; Jackson, 2011), the link between gum-feeding and the presence of clawed digits has not been demonstrated across species with differing degrees of exudativory; secondly, despite the considerable variability in the extent to which callitrichids exploit gums, all possess tegulae. Garber et al. (1996) agree with Cartmill (1979) that the presence of tegulae is an adaptation which simply allows the family to exploit large-diameter vertical supports. Indeed recent studies suggest access to fungi growing on large-diameter substrates is a major consideration for some species (Porter and Garber, 2004; Hilário and Ferrari, 2010).

Studies on non-exudativorous climbing animals (e.g. birds (Pike and Maitland, 2004); lizards (Zani et al., 2000; Ribas et al., 2004; Tulli et al., 2009); carnivores (Van Valkenburgh, 1987)) from both arboreal and saxicolous (rocky) habitats, have demonstrated positive correlations between climbing and claw curvature. More frequent climbing behavior is contingent on a more strongly decurved claw geometry (i.e. Feduccia, 1993). Such findings may bolster suggestions that the presence of tegulae in the callitrichids is largely a result of

climbing requirements *per se* rather than specifically to exudativory. This study will consider differences in tegulae in relation to the ecology of callitrichids in order to clarify the factors underlying the presence of claw-like nails in marmosets and tamarins.

Bicca-Marques (1999) examined hand dimensions in insectivorous callitrichids, and concluded that hand shape is driven by foraging technique, such that: generalist opportunists, gleaning insects and other food from tree trunks and leaf surfaces, had relatively short hands and manipulative foragers searching for insects within crevices had long, slender hands. However, because manipulative insect foraging often occurs on large vertical supports such as tree trunks (Sussman and Kinzey, 1984; Garber, 1992), it is difficult to dissociate the effects of climbing from those of insectivory. Long hands would increase the angle subtended by fingers and thumb when climbing on vertical supports to increase the effective grip on large diameter supports (Cartmill, 1985). Furthermore, postural behaviors such as vertical clinging and trunk-to-trunk leaping, are strongly linked with exudativory and typical on these supports (Garber, 1993; Smith, 1997; Youlatos, 1999a; Garber et al., 2009; Youlatos, 2009). We consider whether intergeneric and interspecific differences in hand and foot morphology are influenced by diet and positional behavior.

A number of arboreal non-primates have patterned, ridged skin on the ventral surfaces of their hands and feet (e.g. tree shrews (*Tupaia glis:* Lemelin, 2000); common dormice (*Muscardinus avellanarius*: Haffner, 1998); raccoons (*Procyon lotor*: Munger and Pubols, 1972); Virginia opossums (*Didelphus virginiana*: Lemelin, 2000); feathertail gliders (*Acrobates pygmaeus*: Rosenberg and Rose, 1999) and koalas (*Phasocolarctos cinereas*: Henneberg et al., 1997)). Such patterns, referred to as dermatoglyphs, are also found in primates and are believed to serve two important functions: first, these patterns enhance the

frictional grip in climbing (Cartmill, 1979; Hamrick, 1998; Lemelin and Jungers, 2007); and second they enhance tactile sensitivity, particularly when associated with the fingertips (Loesch and Martin, 1984; Dominy, 2004). Both functions are not mutually exclusive, indeed both are likely to be important to a climbing animal to assess the physical profile of the surfaces upon which they are moving to prevent slipping (Hoffman et al., 2004). The volar surface dermatoglyphs of callitrichid primates will be examined in consideration of the potential frictional role of epidermal patterning on volar surfaces during climbing and foraging.

Although a number of studies allude to relationships between morphology, positional behavior and exudate foraging in callitrichids, none have considered quantitative relationships with exudativory (Garber and Sussman, 1984; Garber, 1991, 1992, 1993; Bicca-Marques, 1999; Lemelin and Jungers, 2007). Nash and Burrows (2010), discussing the high degree of variability in exudate consumption by callitrichids, identified as an important gap in the current understanding the lack of interspecific morphological comparisons. We analyse data derived from published values in multiple field studies of foraging behaviour alongside morphological data from museum specimens to address this gap focusing on how hand and foot morphology relates to primate diet and food procurement using the Callitrichidae as a model.

METHODS

Skins of 235 adult specimens from 25 species and six extant callitrichid genera (Table 1) were photographed (with a Fujifilm Finepix s5700) at the Natural History Museum, London. Photographs were taken of full pelts from ventral and dorsal perspectives, of the ventral and dorsal aspects of whole hands and feet, and of the tegulae and volar surfaces. To minimise parabolic effects, specimens were laid flat and all photographs were taken from directly above the specimen, at an angle perpendicular to the surfaces. Images were taken from a range of distances (0.2 - 1.5m) with this distance dependent on the level of resolution necessary for the area of interest being photographed. Full pelts were photographed from 0.6 – 1.5 m. To allow measurements to be made from the resultant images, mm grids printed onto clear acetate were placed centrally on the specimen for every individual image taken providing an image-specific calibration point for every photograph. No measurements were taken from the margins of the images.

Specimens used are recorded in the museum catalogue (Napier, 1976) and were wild-caught by a variety of natural history collectors from the early 19th to late 20th century. Current nomenclature was determined by cross-referencing the museum catalogue (Napier, 1976) with more recent systematics (Rylands et al. 2008; Rylands and Mettiermeier 2009). Skins identified in the catalogue as juveniles and those with no information about age but which were significantly below the normal published size ranges for the species were excluded. Data from individual specimens was only included if elements of morphology considered were measurable from the skins, as features in some were obscured by methods of skin preparation and general wear and tear. Specimens from which hand and foot measurements were made had bones still intact within the fingers and toes. This study aimed to extend potential uses of skins, which are a widely available museum resource, to allow direct comparisons of multiple

morphological measures (including soft-tissue measurements) made from a single specimen. Differences between specimens in shrinkage, age and preparation techniques might be expected to introduce error, but analysis of a subset of specimens for which collection measurements of head-body length (HBL) and hindfoot length were available suggests that relative trends in data are unaffected by these. A full list of exact specimens used can be provided by the corresponding author on request.

The photographs taken were used to derive measurements for: HBL (distance measured from tip of nose to proximal base of the tail: Martin et al. 2001)); foot length (from back edge of heel to tip of longest toe: Martin et al. 2001); hand length (from proximal edge of palm to tip of longest finger) and of the longest finger (finger 3) and toe (toe 2) from base of digit to tip (these digits were selected for analysis due to their potential greater influence on prehensile ability, as suggested in Lemelin and Jungers, 2007). All image analyses were carried out using the free Java image processing program, ImageJ (Rasband, 2009).

For each individual, average density of dermatoglyphic ridges was determined from analysis of between five and eight images of 2 mm x 2 mm sections of ventral surfaces of both the hand (palmar) and foot (plantar). Sections were cropped from photographs of palmar and plantar surfaces, using the calibration grid to standardize the size of each section. Ridge widths were measured using ImageJ and used to calculate average number of ridges per mm of hand/foot. Tegula curvature was determined via the method used by Pike and Maitland (2004) for quantification of claw 'hookedness' in raptorial and scansorial birds, and using the angle measuring tool in ImageJ. According to this method, a greater angle corresponds with a more 'hooked' tegula.

An extensive literature search was conducted and data collated on several aspects of species ecology, including: percentage of time spent foraging on different food types, such as fruit, prey, and exudates; percentage of locomotory activity represented by scansorial (vertical climbing) activity and by trunk to trunk leaping; and size and orientation of supports utilized during foraging (Table 2). Studies were included if data was recorded from wild populations and where behaviours were being recorded from single-species troops. Where several studies had comparably collected/described data, average values were calculated. Data were collated from results in the following studies: Garber, 1980[1]; da Fonseca and Lacher, 1984[2]; Garber and Sussman, 1984[3]; Yoneda, 1984[4]a, b; Garber, 1988[5]; Ayres and Clutton-Brock, 1992[6]; Egler, 1992[7]; Ferrari and Strier, 1992[8]; Garber, 1992[9]; Peres, 1992[10]; Rosenberger, 1992[11]; Garber, 1993[12]; Peres, 1993[13]; Lopes and Ferrari, 1994[14]; Peres, 1994[15]; Garber and Pruetz, 1995[16]; Ferrari and Digby, 1996[17]; Dietz et al., 1997[18]; Peres, 1997[19]; Garber, 1998[20]; Hamrick, 1998[21]; Youlatos, 1999a[22]; Araújo et al., 2000[23]; Corrêa et al., 2000[24]; Heymann and Buchanan-Smith, 2000[25]; Heymann et al., 2000[26]; Martins and Setz, 2000[27]; Oliveira and Ferrari, 2000[28]; Garber and Leigh, 2001[29]; Miranda and Faria, 2001[30]; Porter, 2001[31]; Regan et al., 2001[32]; Lehman, 2004[33]; Porter, 2004[34]; Poveda and Sanchez-Palomino, 2004[35]; Raboy and Dietz, 2004[36]; Bicca-Marques, 2005[37]; Garber et al., 2005[38]; Yépez et al., 2005[39]; Cunha et al., 2006[40]; Burity et al., 2007[41]a, b; da Silva and Ferrari, 2007[42]; de Castro and Araújo, 2007[43]; Digby et al., 2007[44]; Garber, 2007[45]; Lapenta and Procópio-de-Oliveira, 2008[46]; Nadjafzadeh and Heymann, 2008[47]; Porter et al., 2007[48]; Raboy et al., 2008[49]; Garber et al., 2009[50]; Garber and Porter, 2009[51]; Porter et al., 2009[52]; Rehg, 2009[53]; Veracini, 2009[54]; Youlatos, 2009[55]; Hilário and Ferrari, 2010[56]; Porter and Garber, 2010[57]; Smith, 2010[58]. Superscript values indicate sources for each of the species as indicated in Table 2.

Statistics were performed in SPSS Version 16.0. Morphological data for genera were compared either using ANOVA or Kruskal-Wallis tests (following tests for equality of variance). Post-hoc comparisons between genera were undertaken using Tukey or Mann-Whitney U tests. All post-hoc tests reported for differences between genera are significant at the $p < 0.05$ level.

RESULTS

Morphological correlates with body size

Callitrichids show an approximate two-fold size range between the smallest (*Cebuella pygmaea)* and largest species (*Saguinus leucopus*) (Table 3). There are significant differences in mean HBL between genera (Table 4). Post-hoc Mann-Whitney U tests identified *Cebuella* as significantly smaller than all other genera and that *Leontopithecus* and *Saguinus* are significantly larger than *Callithrix* and *Mico*. This gives three distinct size categories of: 'small' (*Cebuella*); 'medium' (*Callithrix* and *Mico*) and 'large' (*Callimico, Saguinus* and *Leontopithecus*).

Proportional hand lengths were similar between differently sized species (Table 3). Rates of increase in hand ($HBL^{0.73}$) and finger length ($HBL^{0.73}$) between species, although reduced, are not significantly different from isometric expectations (Table 5: difference from slope of 1: $t_{hand} = 1.30$, 48 d.f., N.S.; $t_{finger} = 1.09$, 48 d.f., N.S.). There are significant differences between genera in proportional hand length and finger length (Table 4). Post-hoc Tukey and Mann-Whitney U tests identify that differences in forelimb dimensions result from *Leontopithecus* having significantly longer fingers and hands than *Callithrix, Cebuella, Mico* and *Saguinus*.

Hindlimb dimensions show smaller species have proportionally longer feet and toes than larger species (Table 3). Foot length and toe length both increase as $HBL^{0.65}$ between species, at a rate significantly less than isometric expectations (Table 5: difference from slope of 1: $t_{foot} = 2.48$, 46 d.f., $p < 0.05$; $t_{toe} = 2.44$, 46 d.f., $p < 0.05$). There are significant differences between genera (Table 4) in both proportional foot length and proportional toe length. Post-hoc Tukey tests identify that these resulted from differences in *Saguinus*, which had significantly shorter feet and toes than *Callithrix, Cebuella* or *Leontopithecus*.

In 18/25 (72%) species the palmar ridge density was greater than the plantar density (Table 3) with this trend being statistically significant for seven species (paired t-tests: *C. jacchus,* $t = -3.06$, 15 d.f., $p < 0.05$; *C. penicillata*, $t = -3.98$, 17 d.f., $p = 0.001$; *M. humeralifer*, $t = -4.63$, 3 d.f., $p < 0.05$; *S. fuscicollis*, $t = -6.22$, 42 d.f., $p < 0.001$; *S. geoffroyi*, $t = -3.69$, 4 d.f.; *S. mystax*, $t = -2.24$, 17 d.f.,; *S. nigricollis,* $t = -2.57$, 11 d.f., $p < 0.05$ for all). There was a marginally non-significant negative trend between body size (HBL) and palmar ridge density across all species though a significant negative correlation with size occurs with plantar ridge density (Table 5). At genus-level, palmar ridge densities are significantly greater than plantar ridge densities (Figure 1) in both Callithrix (paired t-test: $t = 4.12$, 36 d.f., $p < 0.001$) and Saguinus (paired t-test: $t = -6.00$, 119 d.f., $p < 0.001$).

There are significant differences between genera in both palmar ridge densities and plantar ridge densities (Table 4 and Figure 1). Post-hoc Tukey tests identify that *Callimico, Saguinus* and *Leontopithecus* have significantly lower palmar ridge densities than *Callithrix, Cebuella* or *Mico. Callimico* and *Saguinus* have significantly lower plantar ridge densities than *Cebuella, Callithrix* or *Mico* (Figure 1). There are significant differences in palmar ridge densities within *Callithrix* (ANOVA: $F_{3,33} = 6.20$, $p < 0.005$), with *C. aurita* and *C. flaviceps* having significantly lower palmar ridge densities than *C. jacchus* or *C. penicillata*. There were also significant differences in palmar ridge densities for *Saguinus* species (ANOVA: $F_{11,109} = 3.50$, $p < 0.001$), as a result of higher palmar ridge densities in *S. bicolor.*

There is an inverse relationship between tegula curvature and body size such that smaller species have more hooked tegulae (Table 5). Genus-level differences in tegula shape are significant (Table 4), though post-hoc tests do not identify the locations of significant

differences. Significant differences are noted in tegula curvature between the species within *Callithrix* (ANOVA: $F_{3,25} = 4.96$, $p < 0.01$). Post-hoc testing reveals that *C. jacchus* have significantly more curved tegulae than the less exudativorous *C. flaviceps.* Differences in tegula curvature (ANOVA: $F_{10,72} = 2.27$, $p < 0.05$) were also demonstrated within *Saguinus* resulting from increased tegula curvature in *S. leucopus* and *S. martinsi*.

Morphological correlates with ecology

Smaller species exhibit a greater degree of exudativory, scansorial activity and use of vertical supports when foraging (Table 5). Species that use vertical supports to a greater extent during foraging have proportionally longer feet (Fig. 2A: $R = 0.96$, $y = 10.45x - 1.86$, 5 d.f., $p < 0.005$) and more curved tegulae (Fig. 2B: $R = 0.82$, $y = 0.61x - 1.05$, 5 d.f., $p = 0.05$). Species utilising more trunk-to-trunk leaping have longer hands ($R = 0.92$, $y = 13.31x - 2.01$, 6 d.f., $p < 0.005$). More exudativorous species show greater degrees of scansorial activity ($R = 0.89$, $y = 2.01x - 0.11$, 6 d.f., $p < 0.01$) but there were no demonstrable species-level morphological correlates with exudativory. More exudativorous genera have a non-significant tendency towards increased palmar ridge densities (Fig 3A: $R = 0.75$, 5 d.f., N.S.) and a significant increase in plantar ridge densities (Fig. 3B: $R = 0.83$, $y = 1.62x + 3.87$, 5 d.f., $p < 0.05$). No correlations with palmar or plantar ridge density were found with either frugivory or prey capture.

DISCUSSION

Measurements from callitrichids in this study suggest that while relative proportions of the hands were conserved with respect to size, in general, all contributory elements of the feet were proportionally longer in smaller species. Smaller species of callitrichid exhibited greater degrees of exudativory. Consequently, it is to be expected that smaller species will also exhibit behaviors linked more frequently with exudativory, such as scansorial locomotion and use of vertical substrates. Given the greater reliance on exudativory in small species, an increase in relative proportions of the hind feet may confer more support when climbing vertical substrates. Norberg's (1986) evaluation of vertical climbing in the Eurasian tree creeper, *Certhia familiaris*, discusses how lengthening the foot reduces the forces necessary to maintain a grip on a vertical trunk. Furthermore, increasing the length of the foot would act to increase the effective grip while climbing, even without the additional benefit of 'claws' (Cartmill, 1985).

Arboreal primates have unique hand proportions and in particular possess relatively elongated fingers with a greater capacity for prehensility (Kirk et al., 2008). This feature of primates is usually explained as an adaptation to locomotion on small branches, allowing them to create a secure surrounding grip on narrow diameter branches and vines (Lemelin, 1999). As the fingers can bear a significant portion of the weight during locomotion, and since stresses on a digit are suggested to increase in direct proportion to length, expectations are that with increasing size, species should have adaptations for reducing the stress on these digits, such as shortening the functional length (Krakauer et al*.,* 2002) or increasing development of broad, thickened cushion-like pads (described for arboreal rodents in Haffner, 1998). Lemelin and Jungers (2007) study of hand proportions in thirty species of strepsirrhines noted that as body size increases, toes and fingers become proportionally shorter. Such trends may mean that the ability to fully enclose wider diameter branches in an encircling grip is reduced in larger

species, but this might be compensated for by an increased coalescence of volar pads to facilitate frictional force, a trend which is also described in strepshirrines (Lemelin and Jungers, 2007). While callitrichids do not have discrete volar pads, they exhibit a tendency towards shorter finger lengths with increasing size (albeit non-significant) though lower palmar ridge densities are seen with increasing body size in callitrichids, perhaps counter to expectations from comparisons in pad morphology in the strepsirrhines.

However, long, prehensile fingers in primates are also implicated in a greater ability to manipulate objects (Lemelin, 1999). Specialist manipulative foragers such as *Leontopithecus* have longer, narrower hands than other callitrichid genera (Bicca-Marques, 1999), linked to their strategy of foraging in crevices such as bromeliads and tree holes (Dietz et al*.,* 1997). The present study also found that *Leontopithecus* had significantly longer hands (and fingers) than *Callithrix, Cebuella, Mico* and *Saguinus*. *Saguinus* has proportionally shorter hands than other genera. This was in concordance with Bicca-Marques (1999) who separates *Saguinus* into three groups according to hand shape: those with long, narrow hands (*S. fuscicollis, S. nigricollis, S. tripartitus*); those with intermediate shaped hands (*S. bicolor, S. geoffroyi, S. leucopus, S. midas, S. oedipus*) and those with short, wide hands (*S. labiatus, S. mystax*). He suggested that long, narrow hands were related to manipulative foraging for insects. The results of the present study broadly supported these groupings, manipulatively foraging species *S. fuscicollis, S. nigricollis* and *S. tripartitus* (Heymann and Buchanan-Smith, 2000)*,* have long hands compared with many congeners and consumed greater proportions of animal prey.

Stephenson et al.'s (2010) study of comparative hand morphology noted a diversity of claw shapes in galagos, and they suggest that the observed gradient from nail to claw may be evidence of an evolutionary response to allow exploitation of large diameter supports for

exudativory. However, their study did not present any quantitative analysis of either claw curvature or exudativory levels. There is evidence from the present study that exudativory and scansorial activity are correlated, and scansorial species which utilize vertical supports to a greater degree have more hooked tegulae. Youlatos (1999b) examined the positional behavior of six sympatric Ecuadorian primates and also found that small tegulae-bearing callitrichids showed the highest proportions of large vertical support use. This was attributed to requirements for exudativory but, again, no values are given for the proportion of exudates in the different species' diets, supporting only observations in Garber et al. (1996; 2009) that the presence of tegulae in callitrichids is linked to vertical foraging behavior. The advantages of claws and claw-like nails in vertical substrate foraging was suggested to be of particular importance for smaller-bodied species that regularly utilize vertical, large-diameter surfaces, where they facilitate extra grip to compensate for limbs which have too short a reach to allow an effective contact angle to be subtended (Soligo and Martin, 2006; Jackson, 2011).

Bock & Miller (1959) describe how the curvature of the scansorial claw in woodpeckers is key in allowing the tip of the claw to penetrate into the bark of tree trunks. The current study found no direct link between the degree of exudativory and tegula curvature between species, though as seen in Youlatos (1999b), smaller (and more exudativorous) species did have more hooked tegulae. The more exudativorous species of *Callithrix* exhibit greater tegula curvature, trends which are not observed within *Saguinus*. While *Saguinus* are opportunist exudativores, *Calllithrix* are specialists with procumbent incisors to gouge and wound the trees to instigate exudate production. To do this, *Callithrix jacchus* anchor themselves using their upper incisors and then gouge upwards with their lower jaw, which is capable of producing an upwardly directed force equivalent to eight times their own body weight to dig into the tree trunk (Vinyard et al. 2009). Having tegulae with a greater curvature might be expected to increase

interlocking capability with the rough bark substrate, and further help to anchor the monkeys to increase stability on vertical substrates while engaged in gum-feeding. Further, proportionally larger feet in the more exudativorous species, combined with better attachment to the substrate could provide improved leverage to increase gouging efficiency.

Hamrick (2001) found that the breadths of papillary ridges on the toes of didelphid marsupials were wider than on the fingers, i.e. ridge density was greater on the hands. Based on the importance of the hands in tactile exploration, he argued that the increased density of ridges on the hand serves a primarily sensory purpose via an increased distribution of mechanoreceptors. It might be expected, if the key function of ridges on the volar skin is sensory, that ridge density will be higher on the hands. In the majority of callitrichid species, ridge densities *were* higher on the hands than on the feet, lending support to the hypothesis that dermatoglyphic ridges have a function in improving touch discrimination. Such a role would be particularly important to frugivorous primates, that judge fruit ripeness using a combination of cues, including palpating fruit with the hand (Dominy, 2004). Hoffman et al.'s (2004) study of the fingerprints of nine primate species found a positive correlation between the density of sensory cells and frugivory yet the present study found no correlations between frugivory and palmar or plantar ridge densities, although the genera with the lowest values for palmar ridge density here are chiefly frugivorous, perhaps reducing the argument for a chiefly sensory role.

Most primates have greater hindlimb than forelimb contact time when climbing on arboreal supports (Cartmill et al., 2002), so if the purpose of volar skin patterning were to increase friction, as suggested by Haffner's (1998) exploration of the microanatomy of the foot pads of arboreal rodents, it might be expected that ridge densities would be greater on plantar rather than palmar surfaces. On this evidence, the present study's results contradict a frictional

role for dermatoglyphic ridges. However, comparative studies of walking biomechanics have found that, unlike most primates, *C. jacchus* exhibits relatively greater forelimb forces and contact duration when walking (Young, 2009), galloping (Hanna et al., 2006) and climbing (Schmitt, 2003). Cartmill et al. (2002) link longer hindlimb contact to the necessity to maintain a firm grasp on thin flexible supports and, as callitrichids utilize forelimb-powered vertical climbing on large diameter substrates to a significant extent (Hunt et al., 1996), increased frictional contact of the forelimb might be of greater importance. Understanding of the potential frictional role of palmar and plantar ridges in vertical climbing would significantly benefit from consideration of biomechanics of locomotion in other callitrichids. As other vertical climbers, such as the lorises (*Loris* and *Nycticebus*), also exhibit atypical impact forces (Schmitt and Lemelin, 2004), the study of comparative hand/foot dermatoglyphs in primates with typical and atypical gaits and forelimb vs. hindlimb powered climbing would be desirable.

The influence of other locomotor modes on the expression of plantar and palmar dermatoglyphs, may be a key consideration. Although callitrichids are often categorized as generalist arboreal quadrupeds (Connour et al., 2000) evidence from the literature suggests many species utilize leaping locomotion to a significant extent. Observational and biomechanical studies find that jumping in *Saguinus, Callimico, Callithrix* and *Cebuella* is characterized by hindlimb-driven takeoff and forelimb-first landing (Garber, 1991; Garber et al., 2009). It is therefore likely that the forelimbs act to absorb the shock of landing impact in callitrichids (Garber and Leigh, 2001), and will form the initial frictional contact with a substrate to counter slipping. This perhaps provides a further explanation of the increased density of dermatoglyphic ridges on the palms of the hands in comparison to the soles of the feet and potentially also the proportionally longer hands seen in callitrichids which more commonly engage in trunk to trunk leaping in this study. It would be of interest to consider

comparative dermatoglyphs in specialist leaping primates such as indrids and lemurs, which are well studied in terms of jumping biomechanics (Crompton et al., 1993; Demes et al., 1996, 2005), and which land hindlimb-first, to see if patterns in volar skin pattern are reversed.

Smith (2010) suggests generic differentiation in terms of dental specializations for gouging should predict *Cebuella* and *Callithrix* are the most exudativorous, *Saguinus, Leontopithecus* and *Callimico* the least with *Mico* intermediate between the two groups. These expectations are borne out by trends for generic exudate consumption in this study. As there were generic-level correlations between ridge densities on hands and feet and exudativory, ridge density values predict exudativory in a similar way to dental specialization. Significant differences in palmar and plantar ridge densities result from *Callimico*, *Leontopithecus* and *Saguinus* forming a distinct and separate group from *Callithrix*, *Cebuella* and *Mico*.

According to dental adaptations for gouging, *Callithrix* may be further split into three groups (re Natori and Shigehara, 1992): (a) *C. jacchus* and *C. penicillata*; (b) *C. kuhli* and *C. geoffroyi*; *C. aurita* and (c) *C. flaviceps*, in order of decreasing exudativory (Smith, 2010). Our results for palmar ridge densities largely support these groupings of *C. jacchus* and *C. penicillata* with similar values to one another for palmar ridge density, as do *C. aurita* and *C. flaviceps*. Furthermore, *C. aurita* and *C. flaviceps* both have significantly lower palmar ridge densities than either *C. jacchus* or *C. penicillata*. As discussed earlier, tegula curvature is higher in more exudativorous species within this genus, suggesting that ridge density probably has a greater role in gripping, driven by exudate feeding requirements, than in sensory assessment of fruit ripeness. This demonstrates the need for careful consideration of the various facets of a species' ecology which may influence morphology.

Callimico, although genetically closer to *Callithrix, Cebuella* and *Mico* than to *Saguinus* and *Leontopithecus* (Pastorini et al., 1998; Chaves et al., 1999) would not be recognized as such based on dental morphology alone. *Callimico* have not only retained the third molar, a dental feature typically absent from all other callitrichids (Cortés-Ortiz, 2009), but also do not exhibit the specialist incisors typical of the 'gouging' marmosets (see Hill, 1959; Forsythe and Ford, 2011) with which they are a close sister group. The relative morphology of volar surfaces in *Callimico* were similarly problematic and confirmed the difficult-to-resolve position of this genus within the Callitrichidae, ridge densities on both hands and feet suggested they were significantly different from both the marmosets and the tamarins.

To conclude, results suggest that the potential role of volar skin morphology and tegula curvature in the facilitation of exudativory bears further investigation. This is particularly desirable as differences in both reflect trends in dental morphology with relation to levels of exudativory, perhaps via similar evolutionary pressures related to food procurement and food handling. Furthermore, trends in hand and foot dermatoglyph density appeared to group species according to current taxonomy, aligning *Saguinus* with *Leontopithecus* and *Mico* with *Callithrix* and *Cebuella* corroborating the very early tenet of Biegert (1963) who considered the relationship of *Callimico* within the Callitrichidae, argued that combinations of 'cheridial' characters, (features of the hands/feet), including 'claw' presence and extent of frictional volar skin were better taxonomic indicators than dental morphology. Although, it would be difficult to argue based on our findings, that cheridial characters are stronger indicators than dental morphology, the undoubted importance of the role of hand and foot morphology in facilitating food procurement in the callitrichids certainly indicates this warrants further consideration, particularly with respect to differences in reliance on exudativory between species.

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TABLES

Table 1: Museum specimens examined (species and numbers) and species abbreviations used in text and in figures.

Table 2: Values (**average** (*s.e.*) n) calculated from literature for percentage of diet represented by different nutritional sources, locomotor modes (% locomotion observations), and support use (% foraging observations) in 20 species of callitrichid.

Table 3: Head-body lengths, palmar and plantar ridge densities, tegula curvatures and hand and feet measurements relative to head-body length made from museum specimens of 25 species of callitrichid.

Table 4: Summary data for morphological parameters at genus level. Statistics for comparison between genera using ANOVA (unless otherwise indicated: * = Kruskal-Wallis).

Table 5: Species-level correlation statistics between HBL, body dimensions and various aspects of ecology in callitrichids (*log-log relationships; **arcsin-transformed data)

FIGURE LEGENDS

Figure 1: Boxplots of palmar and plantar ridge density in six genera of callitrichid: the marmosets (*Mico*, *Callithrix*, *Cebuella*), *Callimico* and tamarins (*Leontopithecus* and *Saguinus*). Statistics in text.

Figure 2: Relationships between vertical support foraging and (A) proportional foot length and (B) tegula curvature. Statistics in text. Genera symbols □ *Callimico* ○ *Callithrix* △ *Cebuella* ◇ *Leontopithecus* ■ *Mico* ● *Saguinus*. Species abbreviations as in Table 1.

Figure 3: Genus-level relationships between exudate consumption and (A) palmar ridge density and (B) plantar ridge density. Statistics in text. Genera symbols as Figure 2, species abbreviations as in Table 1.

Table 1: Museum specimens examined (species and numbers) and species abbreviations used in text and in figures.

Common name	Scientific name	Authority	Abbreviation	n
Goeldii's monkey	*Callimico goeldii*	Thomas, 1901	Cmg	5
Buffy-tufted marmoset	*Callithrix aurita*	Geoffroy, 1812	Cau	1
Buffy-headed marmoset	*Callithrix flaviceps*	Thomas, 1903	Cfl	3
Common marmoset	*Callithrix jacchus*	Linnaeus, 1758	Cja	17
Black-tufted marmoset	*Callithrix penicillata*	Geoffroy, 1812	Cpe	23
Pygmy marmoset	*Cebuella pygmaea*	Spix, 1823	Ceb	11
Golden-headed lion tamarin	*Leontopithecus chrysomelas*	Kuhl, 1812	Lcr	1
Golden lion tamarin	*Leontopithecus rosalia*	Linnaeus, 1766	Lro	6
Silvery marmoset	*Mico argentata*	Linnaeus, 1766	Mar	3
Gold-and-white marmoset	*Mico chrysoleucus*	Wagner, 1842	Mcr	2
Black-and-white tassel-ear marmoset	*Mico humeralifer*	Geoffroy, 1812	Mhu	4
Golden-white bare-ear marmoset	*Mico leucippe*	Thomas, 1922	Mle	1
Black-tailed marmoset	*Mico melanurus*	Geoffroy, 1812	Mme	6
Pied tamarin	*Saguinus bicolor*	Spix, 1823	Sbi	2
Saddleback tamarin	*Saguinus fuscicollis*	Spix, 1823	Sfu	59
Geoffroy's tamarin	*Saguinus geoffroyi*	Pucheran, 1845	Sge	4
Red-bellied tamarin	*Saguinus labiatus*	Geoffroy, 1812	Sla	11
White-footed tamarin	*Saguinus leucopus*	Günther, 1877	Sle	2
Martin's tamarin	*Saguinus martinsi*	Thomas, 1912	Sma	1
Golden-handed tamarin	*Saguinus midas*	Linnaeus, 1758	Smi	24
Moustached tamarin	*Saguinus mystax*	Spix, 1803	Smy	20
Black-handed tamarin	*Saguinus niger*	Geoffroy, 1803	Snr	11
Black-mantled tamarin	*Saguinus nigricollis*	Spix, 1823	Sns	13
Cottontop tamarin	*Saguinus oedipus*	Linnaeus, 1758	Soe	3

Table 2: Values (**average** (*s.e.*) n) calculated from literature for percentage of diet represented by different nutritional sources, locomotory modes (% locomotion observations), and support use (% foraging observations) in 20 species of callitrichid.

Species	Percentage of diet represented by:			% vertical support use (foraging)	Percentage locomotion:		References
	Fruit	Animal	Exudates		Scansorial	Leaping	
Cmg	**33** (*4.1*) 8	**24** (*5.9*) 8	**7** (*2.0*) 8	**42** (*7.5*) 2	**15** (*0.6*) 3	**55** (-) 1	6, 11, 19, 29, 31, 34, 38, 48, 52, 53, 56
Cau	**23** (*7.0*) 4	**29** (*4.1*) 4	**42** (*7.4*) 6	-	-	-	9,11, 24, 41b, 49, 27, 52, 58
Cfl	**5** (*2.4*) 5	**20** (*2.0*) 6	**65** (*10.3*) 7	-	-	-	8, 11, 17, 24, 49, 52, 56
Cja	**24** (*2.4*) 6	**18** (*2.6*) 7	**55** (*3.0*) 9	-	-	-	9, 11, 17, 21, 23, 40, 43, 44, 49, 50, 52, 56
Cpe	-	**29** (-) 1	**57** (*13.5*) 3	-	-	-	2, 11, 30
Ceb	-	**22** (*11.0*) 2	**69** (*2.1*) 2	**60** (*37*) 2	**36** (*6.3*) 3	**37** (-) 1	6, 8, 9, 11, 13, 22, 55, 38, 39, 44 ,45, 50, 52
Lcr	**82** (-) 1	**14** (-) 1	**7** (-) 1	-	-	-	8, 9, 11, 41a
Lro	**77** (*7.7*) 3	**15** (*0.4*) 4	**1** (*0.6*) 4	-	-	-	8, 9, 56, 11, 18, 21, 36, 44, 46
Mar	**36** (-) 1	**5** (-) 1	**59** (-) 1	-	-	-	6, 24, 54
Mhu	-	-	**27** (-) 1	-	-	-	6, 9, 52
Sbi	**39** (-) 1	**59** (-) 1	**1** (-) 1	-	-	-	7
Sfu	**59** (*5.6*) 10	**23** (*6.4*) 10	**14** (*2.4*) 10	**33** (-) 1	**16** (*1.4*) 3	**32** (*8.8*) 2	4b, 5, 6, 8, 9, 10, 11, 12, 13, 14, 16, 25, 26, 29, 31, 34, 37, 38, 44, 47, 53, 57
Sge	**44** (*6.2*) 3	**31** (*8.9*) 3	**20** (*5.2*) 3	**13** (-) 1	-	**4** (-) 1	1, 9, 11, 38, 57
Sla	**68** (*8.1*) 4	**11** (-) 2	**11** (*2.0*) 3	**19** (-) 1	**6** (*0.5*) 2	**8** (*0.2*) 2	4a, 8, 11, 25, 29, 53, 31, 32, 34, 37, 38, 52
Sle	**83** (-) 1	**12** (-) 1	**0** (-) 1	-	-	-	35
Smi	**56** (*8.5*) 2	**31** (-) 1	**5** (-) 1	-	-	-	6, 9, 32, 33, 45
Smy	**54** (*5.6*) 8	**33** (*7.2*) 9	**8** (*2.5*) 9	**13** (*4.2*) 4	**3** (*0.4*) 2	**10** (*0.9*) 2	5, 8, 9, 10, 11, 12, 13, 15, 16, 20, 25, 26, 37, 38, 44, 47, 52, 57, 58
Snr	**84** (*6.9*) 3	**7** (*1.5*) 3	**13** (*10.4*) 2	-	-	-	11, 28, 42, 57
Soe	**38** (-) 1	**39** (-) 1	**14** (-) 1	-	**17** (-) 1	-	3, 9, 21, 52
Str	**40** (*21.5*) 2	**48** (*26.5*) 2	**12** (-) 1	-	**16** (-) 1	**18** (-) 1	38, 45, 57

Table 3: Head-body lengths, palmar and plantar ridge densities, tegula curvatures and hand and feet measurements relative to head-body length made from museum specimens of 25 species of callitrichid.

					Lengths as proportion of HBL			
Species	HBL (mm)	Palmar ridge density (ridges/mm)	Plantar ridge density (ridges/mm)	Tegula curvature (º)	Hand	Finger	Foot	Toe
Cmg	**247** (*20*) 5	**4.0** (*0.16*) 5	**3.7** (*0.20*) 5	**138** (*6.9*) 4	**0.19** (*0.014*) 5	**0.063** (*0.005*) 5	**0.22** (*0.014*) 5	**0.069** (*0.004*) 5
Cau	**278** (-) 1	**3.9** (-) 1	**4.7** (-) 1	**103** (-) 1	**0.14** (-) 1	**0.056** (-) 1	**0.21** (-) 1	**0.068** (-) 1
Cfl	**270** (*20*) 2	**4.1** (*0.70*) 2	**4.3** (*0.60*) 2	**116** (*3.9*) 2	**0.16** (*0.007*) 3	**0.056** (*0.004*) 3	**0.23** (*0.013*) 3	**0.070** (*0.002*) 3
Cja	**226** (5) 16	**5.3** (*0.13*) 16	**4.8** (*0.14*) 16	**139** (*3.8*) 11	**0.16** (*0.004*) 17	**0.059** (*0.002*) 17	**0.22** (*0.006*) 17	**0.070** (*0.003*) 17
Cpe	**220** (*3*) 18	**5.3** (*0.09*) 18	**4.8** (*0.09*) 18	**135** (*2.7*) 15	**0.16** (*0.005*) 23	**0.060** (*0.002*) 23	**0.22** (*0.005*) 23	**0.070** (*0.002*) 23
Ceb	**143** (*4*) 11	**5.2** (*0.14*) 11	**5.0** (*0.17*) 11	**144** (*3.8*) 5	**0.18** (*0.007*) 11	**0.072** (*0.003*) 11	**0.23** (*0.008*) 11	**0.077** (*0.004*) 11
Lcr	**239** (-) 1	**4.3** (-) 1	**5.1** (-) 1	**145** (-) 1	**0.29** (-) 1	**0.098** (-) 1	**0.26** (-) 1	**0.082** (-) 1
Lro	**278** (*11*) 6	**4.5** (*0.15*) 6	**4.2** (*0.12*) 6	**-**	**0.20** (*0.013*) 6	**0.071** (*0.003*) 6	**0.23** (*0.013*) 6	**0.075** (*0.006*) 6
Mar	**216** (*15*) 3	**5.1** (*0.65*) 3	**5.1** (*0.17*) 3	**133** (*3.0*) 2	**0.17** (*0.012*) 3	**0.056** (*0.004*) 3	**0.22** (*0.015*) 3	**0.073** (*0.007*) 3
Mcr	**193** (*15*) 2	**4.8** (*0.35*) 2	**5.2** (*0.10*) 2	**137** (-) 1	**0.21** (*0.025*) 2	**0.076** (*0.007*) 2	**0.28** (*0.067*) 2	**0.079** (*0.017*) 2
Mhu	**247** (*9*) 4	**5.2** (*0.19*) 4	**4.7** (*0.11*) 4	**145** (*4.0*) 3	**0.16** (*0.004*) 4	**0.051** (*0.001*) 4	**0.21** (*0.015*) 4	**0.067** (*0.004*) 4
Mle	**213** (-) 1	**4.9** (-) 1	**5.5** (-) 1	**137** (-) 1	**0.16** (-) 1	**0.062** (-) 1		
Mme	**247** (*10*) 8	**5.3** (*0.41*) 4	**4.8** (*0.26*) 4	**147** (*9.5*) 3	**0.16** (*0.004*) 6	**0.059** (*0.003*) 6	**0.21** (*0.006*) 6	**0.062** (*0.004*) 5
Sbi	**240** (*34*) 2	**6.3** (*0.85*) 2	**4.9** (*0.25*) 2	**118** (*1.1*) 2	**0.16** (*0.004*) 2	**0.063** (*0.007*) 2	**0.21** (*0.038*) 2	**0.069** (*0.011*) 2
Sfu	**243** (*3*) 43	**4.7** (*0.07*) 43	**4.2** (*0.06*) 14	**134** (*2.2*) 36	**0.17** (*0.003*) 59	**0.060** (*0.001*) 63	**0.21** (*0.003*) 59	**0.065** (*0.001*) 59
Sge	**262** (*10*) 5	**5.1** (*0.19*) 5	**4.3** (*0.23*) 15	**129** (*9.3*) 2	**0.16** (*0.012*) 4	**0.056** (*0.005*) 5	**0.21** (*0.018*) 4	**0.064** (*0.007*) 5
Sla	**256** (*8*) 9	**4.7** (*0.19*) 9	**4.9** (*0.20*) 16	**133** (*5.3*) 7	**0.16** (*0.007*) 11	**0.059** (*0.004*) 11	**0.19** (*0.011*) 11	**0.057** (*0.004*) 11
Sle	**298** (17) 2	**4.2** (*0.35*) 2	**3.7** (*0.10*) 17	**147** (*7.5*) 2	**0.16** (*0.004*) 2	**0.054** (*0.005*) 2	**0.19** (*0.017*) 2	**0.066** (*0.001*) 2
Sma	**226** (-) 1	**4.6** (-) 1	**4.1** (-) 18	**146** (-) 1	**0.23** (-) 1	**0.081** (-) 1	**0.21** (-) 1	**0.068** (-) 1
Smi	**283** (*6*) 15	**4.9** (*0.13*) 15	**4.7** (*0.15*) 19	**120** (*4.8*) 13	**0.17** (*0.009*) 24	**0.057** (*0.003*) 25	**0.19** (*0.004*) 24	**0.061** (*0.001*) 25
Smy	**270** (*6*) 18	**4.8** (*0.10*) 18	**4.5** (*0.14*) 20	**110** (*12.5*) 2	**0.15** (*0.005*) 20	**0.055** (*0.002*) 24	**0.20** (*0.005*) 20	**0.053** (*0.003*) 20
Snr	**278** (*6*) 10	**4.9** (*0.14*) 10	**4.5** (*0.17*) 21	**123** (*4.9*) 10	**0.16** (*0.006*) 11	**0.059** (*0.004*) 11	**0.20** (*0.007*) 11	**0.063** (*0.003*) 11
Sns	**265** (*8*) 12	**4.7** (*0.12*) 12	**4.2** (*0.16*) 22	**135** (*4.0*) 7	**0.16** (*0.006*) 13	**0.059** (*0.002*) 13	**0.18** (*0.009*) 13	**0.054** (*0.004*) 13
Soe	**255** (*15*) 2	**3.8** (*0.10*) 2	**4.4** (*0.45*) 23	**-**	**0.16** (*0.004*) 3	**0.062** (*0.005*) 3	**0.26** (*0.025*) 3	**0.069** (*0.006*) 3
Str	**239** (*28*) 2	**4.6** (*0.25*) 2	**4.4** (*0.15*) 24	**123** (*7.2*) 2	**0.17** (*0.013*) 2	**0.077** (*0.008*) 2	**0.22** (*0.008*) 2	**0.071** (*0.009*) 2

Table 4: Summary data for morphological parameters at genus level. Statistics for comparison between genera using ANOVA (unless otherwise indicated: * = Kruskal–Wallis).

	Genus						Comparison	
	Callimico	Callithrix	Cebuella	Leontopithecus	Mico	Saguinus	Statistic	p <
Size class	Large	Medium	Small	Large	Medium	Large		
Head-body length (mm)	**246** (*20*) 5	**227** (4) 37	**142** (4) 11	**272** (10) 7	**231** (7) 15	**260** (2) 120	76.93*	0.001
Palmar ridge density (no/mm)	**4.00** (*0.16*) 5	**5.19** (*0.10*) 37	**5.23** (*0.14*) 11	**4.44** (*0.13*) 7	**5.26** (*0.21*) 15	**4.74** (*0.04*) 120	9.88	0.001
Plantar ridge density (no/mm)	**3.66** (*0.20*) 5	**4.81** (*0.08*) 37	**5.03** (*0.17*) 11	**4.29** (*0.17*) 7	**4.93** (*0.10*) 15	**4.39** (*0.05*) 120	9.68	0.001
Tegula curvature (º)	**138.1** (*6.88*) 4	**134.0** (*2.50*) 29	**144.5** (*3.76*) 5	**145.4** (-) 1	**139.6** (*3.61*) 11	**129.7** (*1.66*) 83	2.78	0.05
Hand length/HBL	**0.18** (*0.014*) 5	**0.16** (*0.003*) 37	**0.18** (*0.006*) 11	**0.21** (*0.02*) 7	**0.17** (*0.005*) 16	**0.16** (*0.002*) 152	6.57	0.001
Foot length/HBL	**0.22** (*0.014*) 5	**0.22** (*0.004*) 44	**0.23** (*0.008*) 11	**0.23** (*0.01*) 7	**0.22** (*0.01*) 15	**0.20** (*0.002*) 152	6.89	0.001
Finger length/HBL	**0.063** (*0.005*) 5	**0.059** (*0.001*) 44	**0.072** (*0.003*) 11	**0.075** (*0.005*) 7	**0.059** (*0.002*) 16	**0.058** (*0.001*) 164	22.70*	0.001
Toe length/HBL	**0.069** (*0.004*) 5	**0.070** (*0.002*) 44	**0.077** (*0.004*) 11	**0.076** (*0.005*) 7	**0.068** (*0.003*) 15	**0.061** (*0.001*) 154	8.38	0.001

Table 5: Species-level correlation statistics between HBL, body dimensions and various aspects of ecology in callitrichids (*log-log relationships; **arcsin-transformed data)

HBL vs.	R	df	p<	Equation
Hand length*	0.56	24	0.01	y = 0.68x - 0.007
Finger length*	0.50	24	0.01	y = 0.72x - 0.496
Foot length*	0.73	24	0.001	y = 0.65x + 0.164
Toe length*	0.41	24	0.05	y = 0.62x - 0.301
Palmar ridge density	0.38	24	0.06	NS
Plantar ridge density	0.56	24	0.01	y = -0.008x + 6.49
Tegulae (radians)	0.51	22	0.05	y = -0.003x + 3.08
Exudativory**	0.46	19	0.01	y = -0.005x + 1.42
Scansorial activity**	0.91	7	0.01	y = -0.003x + 0.76
Vertical supports**	0.84	5	0.05	y = -0.003x + 1.01

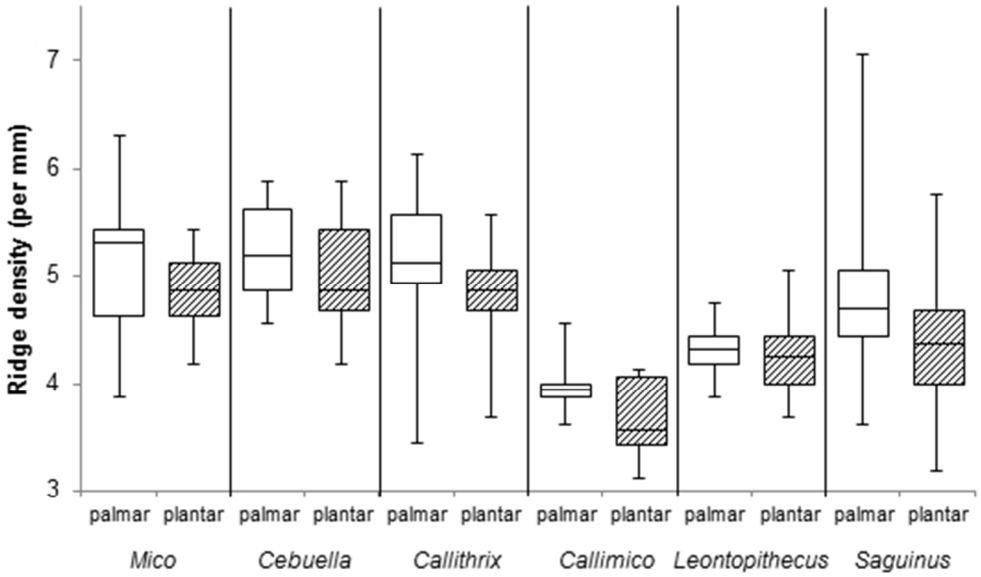

Fig. 1
143x91mm (96 x 96 DPI)

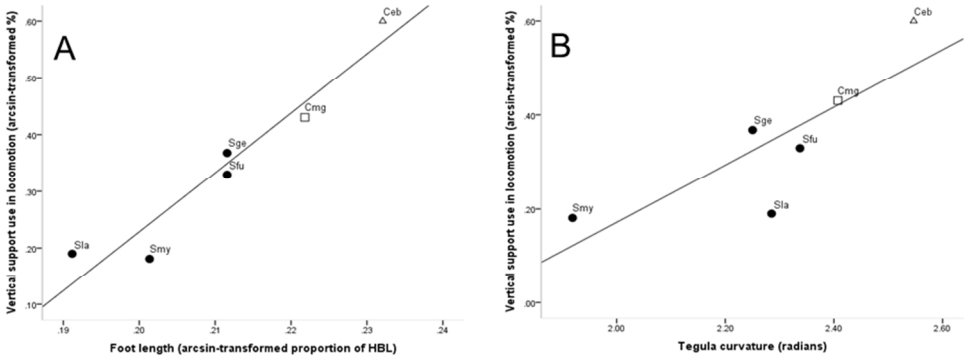

Fig. 2
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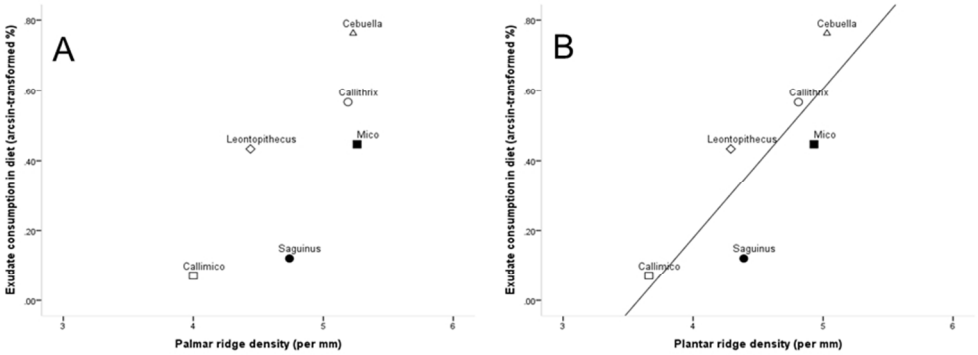

Fig. 3
254x93mm (96 x 96 DPI)